kindly read the manuscript. — UNIVERSITY OF KENTUCKY, LEXINGTON, KENTUCKY.

Literature Cited

Abrams, L. 1940. Illustrated Flora of the Pacific States. v. 1. Stanford University Press, Stanford, Calif.

Braun, E. Lucy. 1943. An Annotated Catalog of the Spermatophytes of Kentucky. Cincinnati, The Author.

Fernald, M. L. 1950. Gray's Manual of Botany, ed. 8. American Book Co., New York.

Galway, Desma H. 1945. The North American Species of *Smilacina*. Amer. Midl. Nat. **33**: 644-666.

Gleason, H. A. 1952. The New Britton and Brown Illustrated Flora. N. Y. Bot. Gard., New York.

Harper, R. M. 1905. Phytogeographical Explorations in the Coastal Plain of Georgia in 1904. Bull. Torrey Bot. Club **32**: 451-457.

———— 1906. A Phytogeographical Sketch of the Altamaha Grit Region of the Coastal Plain of Georgia. Ann. N. Y. Acad. Sci. 17: 1-414.

McFarland, F. T. 1942. A Catalogue of the Vascular Plants of Kentucky. Castanea **7**: 77-108.

Small, J. K. 1933. Manual of the Southeastern Flora. The Author, New York.

HYBRID ASPENS IN THE LOWER PENINSULA OF MICHIGAN[1]

Burton V. Barnes[2]

INTRODUCTION

One explanation for the polymorphism and diversity found in the aspens, *Populus tremuloides* Michaux and *P. grandidentata* Michx., is an exchange of genes between these species through hybridization and backcrossing. Anderson (1949) and others have demonstrated the importance of introgression as a vital force in evolution. In a study of the natural variation and clonal development of the aspens in the Lower Peninsula of Michigan I searched for hybrids on two research sites on forest land of the University of Michi-

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gan Biological Station, near Pellston, Michigan, and in other parts of Lower Michigan.[3] In this paper I shall list and describe aspen hybrids and putative introgressants discovered in the Lower Peninsula of Michigan and shall discuss briefly the ubiquity of the *P. grandidentata* × *P. tremuloides* hybrid in southeastern Michigan as compared with its apparent rarity in the northernmost part of Lower Michigan.

HYBRIDS AND INTROGRESSANTS

POPULUS GRANDIDENTATA × TREMULOIDES

A hybrid between *P. grandidentata* and *P. tremuloides* was first reported and described by Victorin (1930). Heimburger (1936) produced hybrid plants by crossing the two species. He reported a scarcity of natural *grandidentata-tremuloides* hybrids and said this might be explained by the fact that "*P. tremuloides* flowers about a week to ten days before *P. grandidentata* in nature." Pauley (1956) reported that *P. tremuloides* flowered from 10 to 14 days before *P. grandidentata* and stated that the hybrids were not infrequent in central and eastern Massachusetts. He had observed scattered hybrid individuals and hybrid swarms as well as what were presumed to be F_2 plants or backcrosses to one of the parents.

In April 1956 I discovered one hybrid clone on an abandoned field in Section 17, T. 10 N., R. 6 E., Saginaw County, Michigan. This hybrid was tentatively identified on the basis of the scattered hairs that were found on the terminal and lateral bud scales. Fallen leaves collected at the base of several trees in the group closely resembled the hybrid leaves illustrated by Pauley (1956).

A second hybrid was discovered in October 1957 on the forest land of the University of Michigan Biological Station (NW1/2, Section 25, T. 37 N., R. 4 W., Emmet County). The 13 living ramets of this clone were severely damaged by hypoxylon canker and were apparently unable to compete successfully with vigorous neighboring clones of quaking and bigtooth aspen. In August 1958 Dr. Warren H. Wagner,

[3]Barnes, Burton V. 1959. Natural variation and clonal development of *Populus tremuloides* and *P. grandidentata* in Northern Lower Michigan. 334 pp. Unpublished.

Jr., discovered a hybrid swarm in Monroe County. Consequently, in the fall of 1958 a more intensive search for hybrids was directed in southeastern Michigan. Thirty hybrid clones and putative introgressants were discovered in eight 3- to 8-hour trips. Many more hybrid clones could be located by systematic search in southeastern Michigan. Dr. Wagner located five additional clones in 1960. Hybrid clones have now been located in 10 counties of Michigan's lower peninsula. Location of these hybrid clones and putative introgressants is shown in the Appendix. Specimens of these will be deposited in the University of Michigan Herbarium.

Hybrids are typical in many localities in southeastern Michigan where the parent species occur. The number of hybrid clones is estimated at from 1 to 5 percent of those present in the localities observed. On the University of Michigan Biological Station land, however, the frequency is much lower, and this seems to be true for the entire Douglas Lakes area of the northern tip of the Lower Peninsula.

The apparent abundance of the hybrid in Lower Michigan may be due to several factors. The difference in flowering time between bigtooth and quaking aspen may not be as great as one might suspect. I can offer no proof, however, that this barrier is stronger in northern Michigan than in southeastern Michigan. I did observe numerous receptive female flowers on several *P. tremuloides* clones near Pellston, Michigan, at the time when *P. grandidentata* pollen was being discharged. These flowers were usually located at the base or tip of a catkin and represent an intraclonal lag in flowering. Einspahr and Joranson (1960) reported a somewhat similar intraclonal lag in flowering for seven aspen clones when their flower buds were forced to develop in the greenhouse. This intraclonal lag was apparently verified on only one tree under natural conditions. This developmental phenomenon may be closely related to the early-late leaf situation described by Critchfield (1960). Late flowering may be largely restricted to greenhouse conditions because not all flower buds may be in the same developmental stage when branches are collected 4 to 6 weeks before normal flowering time.

While intraclonal variation might explain the source of receptive female *P. tremuloides* flowers, there are at least two other explanations. Pauley (1956) pointed out that in areas of temperature inversion the flowering of female *P. tremuloides* clones may be retarded until it corresponds with the flowering time of neighboring *P. grandidentata* clones. Recognizing the wide range in the variability of both species, interclonal differences in flowering time might also account for pollination of *P. tremuloides* flowers by *P. grandidentata.*

Establishment of aspen seedlings is extremely difficult *(ibid.)*. This may be the reason why the hybrid is apparently much more abundant in southeastern Michigan than in the northern tip of the Lower Peninsula. In southeastern Michigan many hybrid clones were discovered in abandoned fields or along the edge of cultivated fields where they bordered a woodlot. There appears to be more repeated disturbance, primarily by cultivation, in southeastern Michigan than on University of Michigan Biological Station property and surrounding areas. More disturbance, coupled with more fertile soil and a somewhat more moderate climate in southeastern Michigan, probably means that the establishment of seedlings is easier.

Most ramets of the hybrid clones were not more than 2 or 3 inches in diameter at breast height and were probably younger than 20 years in age. Leaf samples from 25 of the hybrid clones were measured and examined in detail.[4] In general, the size of the hybrid leaves is intermediate between that of the parent species. The leaf shape of the hybrid clones varies as much as that within either of the parent species. To illustrate part of the variation among hybrid clones, two leaves typical of eight hybrid clones and typical leaves of the parent species are pictured in Fig. 1.

INTROGRESSION

Introgression, the flow of genes from one species into another through repeated backcrossing to either parent, has

[4]At least 50 leaves from each hybrid clone were measured to obtain the mean blade width, blade length, and petiole length. The number of teeth along both margins of at least 30 leaves of each clone was counted.

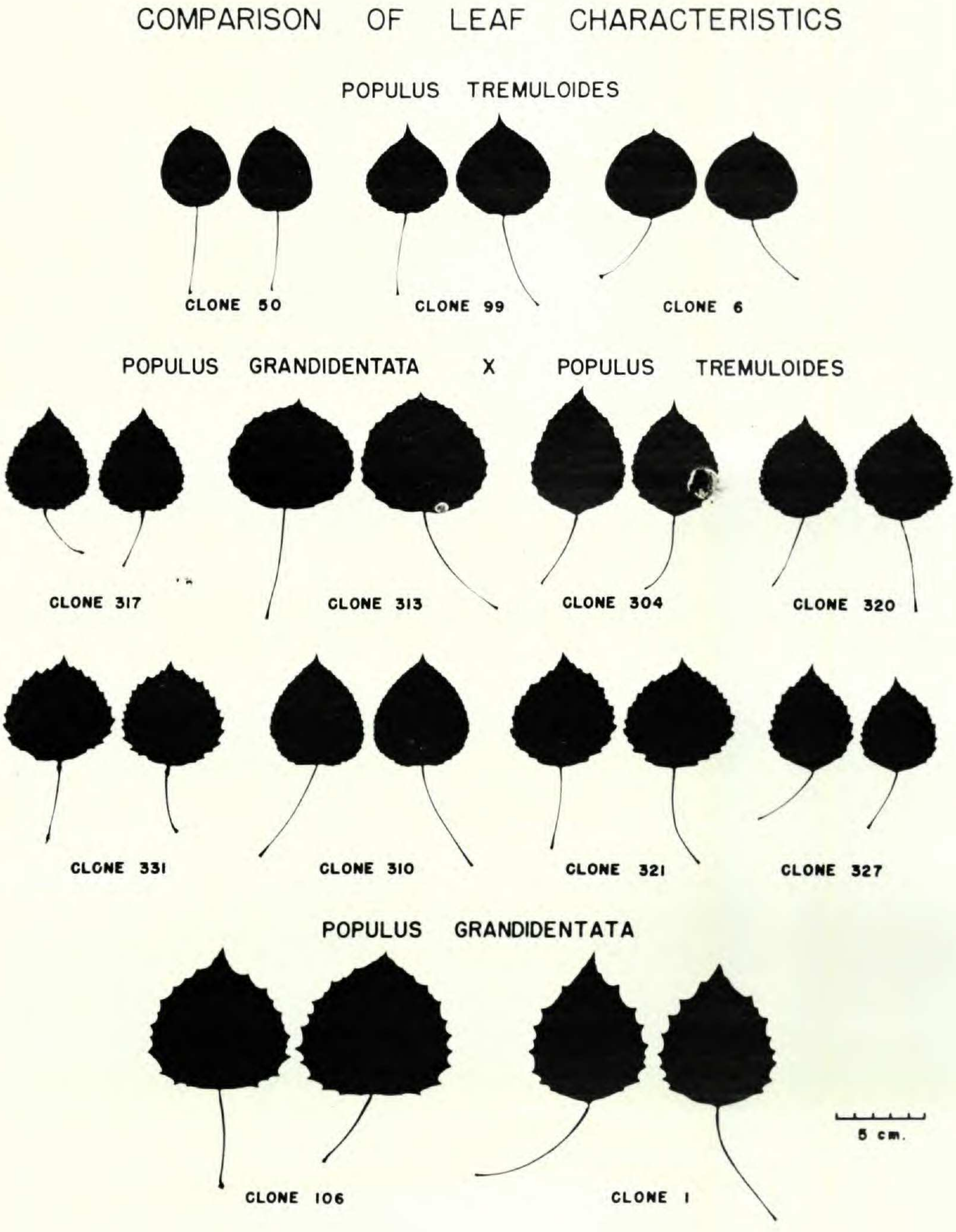


Figure 1

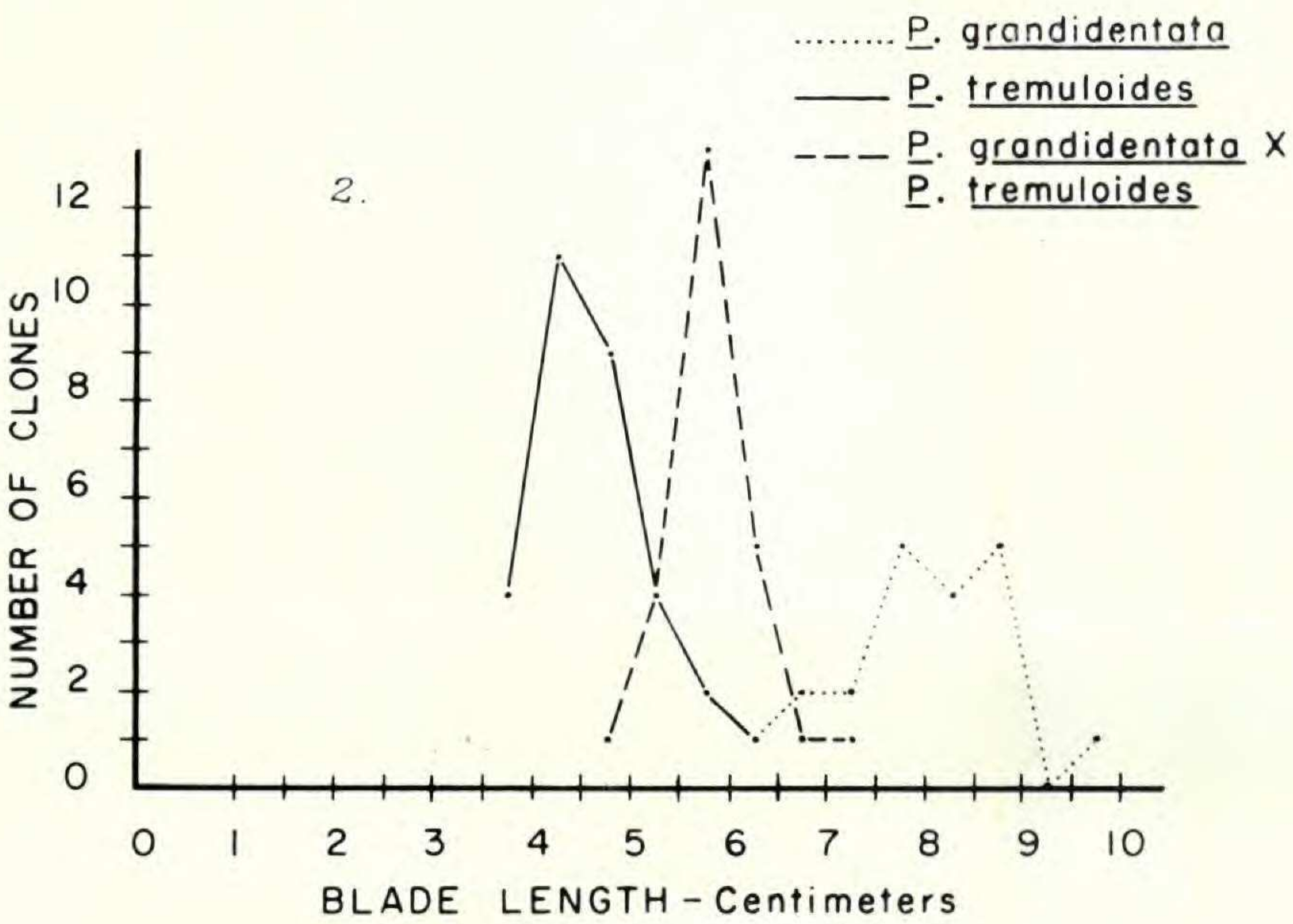
Comparison of leaf characteristics of *P. tremuloides*, *P. grandidentata*, and hybrids.

been described in *Acer* (Desmarais, 1952), *Quercus* (Cooperrider, 1957), and in several other plant genera (Anderson, 1949, 1953; Stebbins, 1950). A few hybrids collected in southeastern Michigan closely resemble *P. tremuloides*, yet have several characteristics of *P. grandidentata*. A series of frequency polygons illustrates leaf differences between the hybrids and the parent species (Figs. 2, 3, 4, 5). Since leaf specimens were not collected from the parents in southeastern Michigan, data from the aspen clones studied intensively in the forest of the University of Michigan Biological Station were used (Barnes, 1959). The hybrid clones are more nearly like *P. tremuloides* in respect to blade width, blade length, and petiole length. The number of teeth per leaf side, however, corresponds more closely to *P. grandidentata*. Of the four characters illustrating the intermediacy of the hybrid clones, the number of teeth per leaf side and the blade length are the most explicit quantitative characters separating hybrids from the parent species.

Hairiness of the terminal and lateral bud is one of the most striking differences between *P. tremuloides* and *P. grandidentata*. This character, however, lends itself less easily to quantification than the four leaf attributes. Anderson (1957), with a semigraphical method, used four of the more distinct features to characterize the differences among clones of the hybrids and parent species (Fig. 6). The hybrids are intermediate between the two parents, but they resemble *P. tremuloides* more closely than *P. grandidentata*. Three of the putative hybrid clones are suspected as being introgressants or backcrosses (clones 310, 317, and 333).

Without additional study and analysis of the parent and hybrid populations in southeastern Michigan, one can report only that the leaf characteristics of several hybrid clones closely resemble *P. tremuloides*. Usually, F_1 hybrids between distinct species are uniform in their characteristics, while segregates appear in the second and following generations (Anderson, 1949). However, the variation within both parents is so diverse and as yet only so summarily described, that F_1 plants seeming to resemble *P. tremuloides* in one, two, or more characteristics might be expected in the F_1 generation.

Sympatric introgression may occur between two distinct species that are ecologically or physiologically separated.



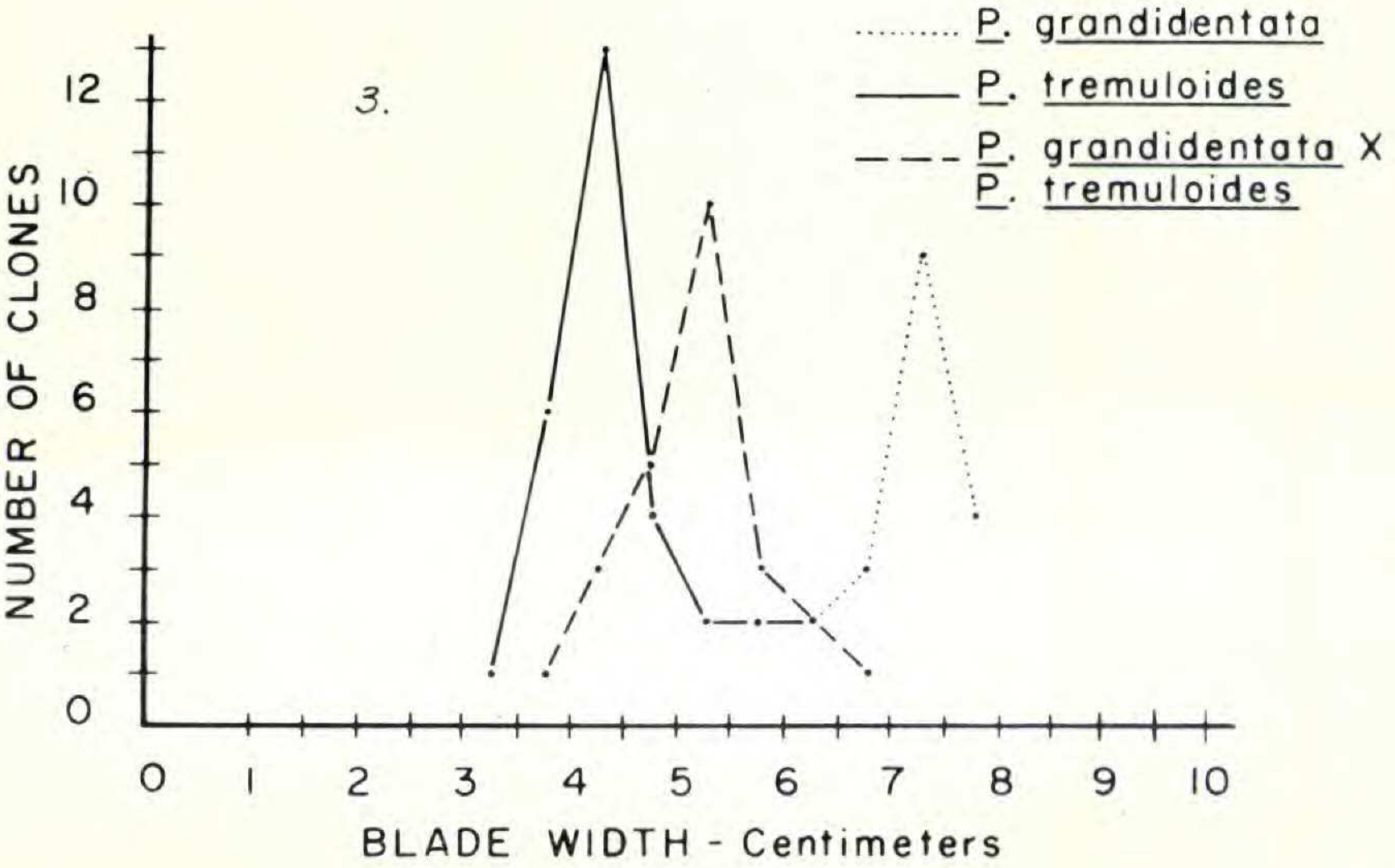


FIG. 2. Frequency polygons illustrating differences in blade length for clones of the hybrid and the parent species.

FIG. 3. Frequency polygons illustrating differences in blade width for clones of the hybrid and the parent species.

Anderson (1948, 1949) pointed out that where the species are separated by habitat requirements, only when the "habitat is hybridized" can the F_1 hybrids find an ecological condition suitable for establishment and survival. In succeeding generations, according to Anderson (1949), the hybrids segregate but the habitat usually does not. Thus, hybrid plants possessing about the same habitat requirements of either of the parent species, i.e. backcrosses to either parent, are favored over F_2 or successive generation segregates. *P. tremuloides* and *P. grandidentata*, however, are not isolated ecologically by their habitat requirements. The habitat of *P. tremuloides* overlaps that of *P. grandidentata*, and both species are frequently growing together on the same site. Therefore, disturbance by man or natural agents, is probably more important as a prerequisite to seedling establishment than "hybridizing the habitat." Thus, it is probable that in southeastern Michigan, F_1 and F_2 hybrids, as well as introgressants, would be about equally fitted for a given habitat that is suitable for both parents.

The variability of the parental species, *P. tremuloides* and *P. grandidentata*, may be due to multiple alleles for genes in the gene pool, mutation, drift, and introgression. Without further analysis it is difficult to say what combination of these factors is responsible for the polymorphism exhibited by the two species.

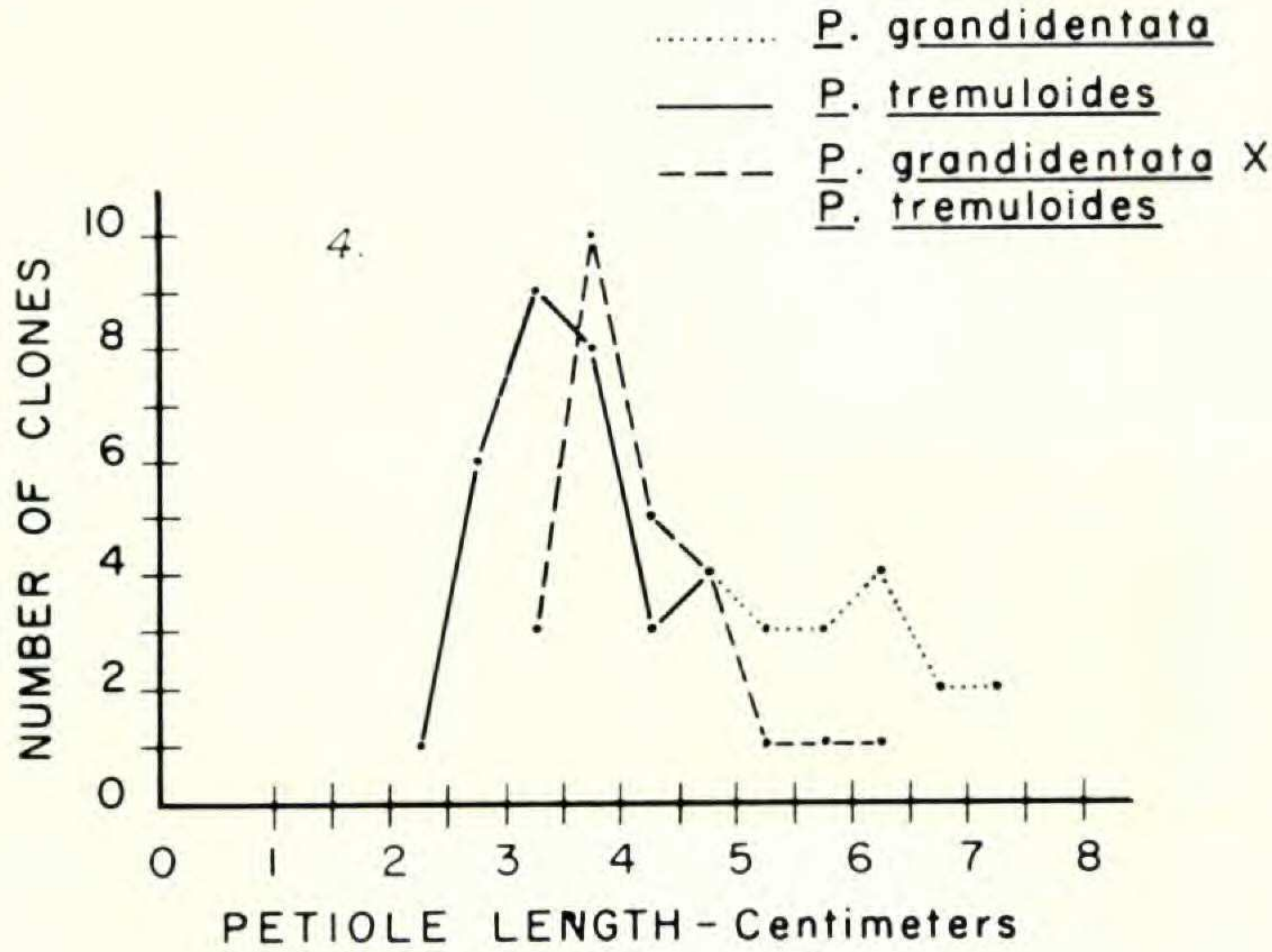
POPULUS ALBA × TREMULOIDES

Two individuals of the *P. alba* × *tremuloides* hybrid were discovered in the Lower Peninsula. One clone was located at the edge of an abandoned field near the juncture of Woods Road and Highway M-18 (SE1/4, SE 1/4, Section 23, T. 23 N., R. 2 W., Gladwin County. The form of this tree resembles that of *P. tremuloides* rather than *P. alba* trees in Lower Michigan.

A second *P. alba* × *tremuloides* hybrid was discovered along the Deckerville Road, S1/2, Section 30, T. 13 N., R. 10 E., Tuscola County. This hybrid was recognized by its extremely shiny green leaves and its silvery bark.

P. alba × *P. tremuloides* hybrids were reported in Canada by Heimburger (1936) and Peto (1938). According to Peto, the *P. alba* × *tremuloides* hybrid was not as frequent as the *alba* × *grandidentata* hybrid in the vicinity of Ottawa, Canada.

The leaves of the *P. alba* × *tremuloides* hybrid are intermediate in shape and serration between the parents. *P. alba* leaves are palmately lobed and tomentose on the undersurface. The margin of *P. alba* leaves is irregularly and shallowly serrate. The leaves of the hybrid are not lobed but are irregularly toothed. The teeth of the hybrid leaves resemble



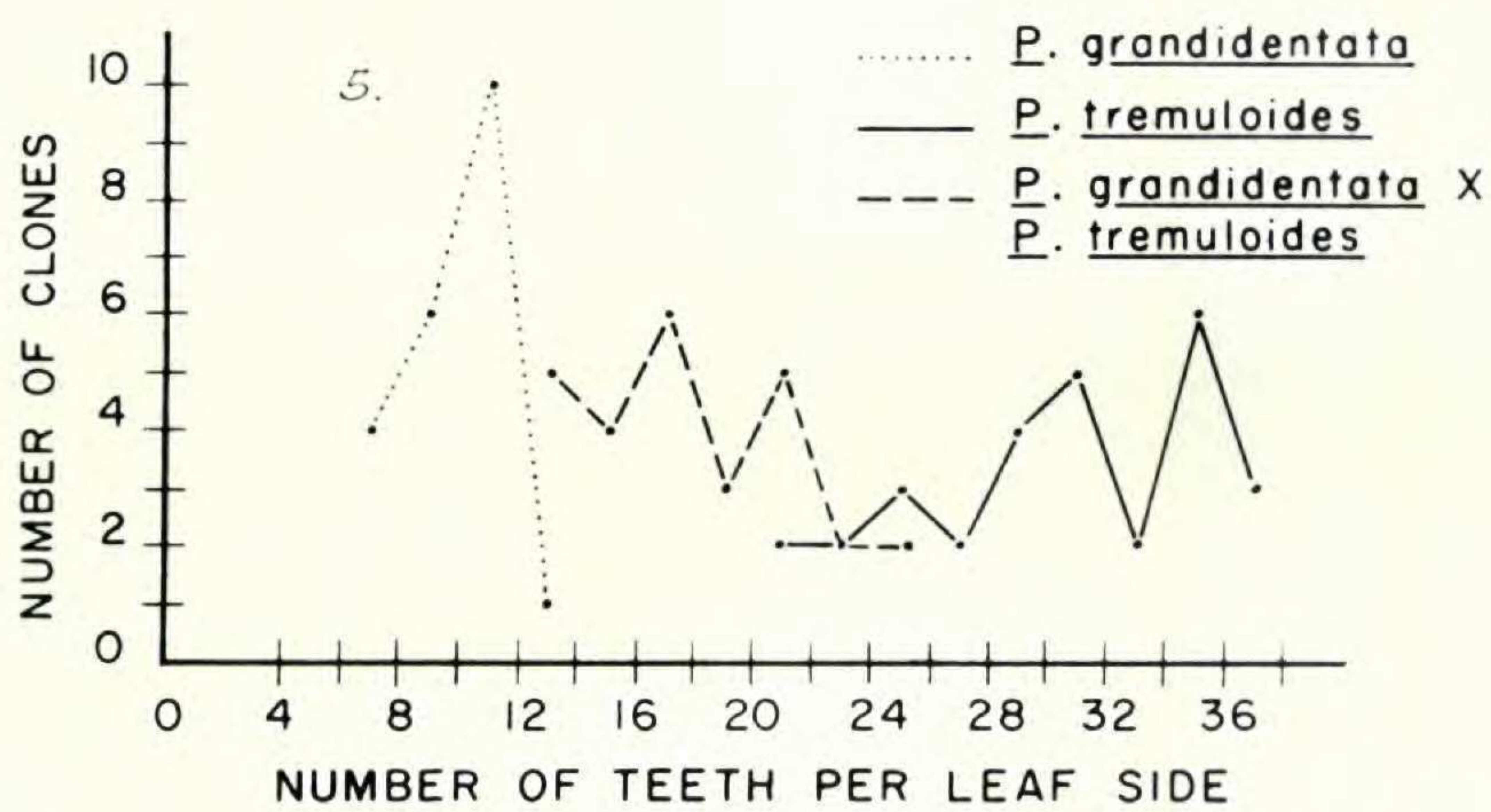


FIG. 4. Frequency polygons illustrating differences in petiole length for clones of the hybrid and the parent species.

FIG. 5. Frequency polygons illustrating differences in number of teeth per leaf side for clones of the hybrid and the parent species.

those of *P. tremuloides* more than those of *P. alba*. The numbers of teeth per leaf side for the Gladwin and Tuscola County hybrids were 14.6 and 15.1, respectively. The under-side of the immature leaves of the hybrid is moderately tomentose and becomes glabrous as the leaves mature.

Buds of the hybrids were covered with a tomentum that was not as dense as the tomentum on buds of *P. alba*. The immature shoots were also covered with a moderate amount of tomentum that did not entirely disappear from the new shoots during their initial year. The bark of the hybrid had many diamond-shaped cracks — a typical characteristic of *P. alba* trees of the same size. The bark was rougher in texture and more silvery-white in color than bark of typical sapling or pole-size trees of *P. tremuloides*.

Catkins collected from the hybrid in Gladwin County were predominantly male, but some female flowers were discov-

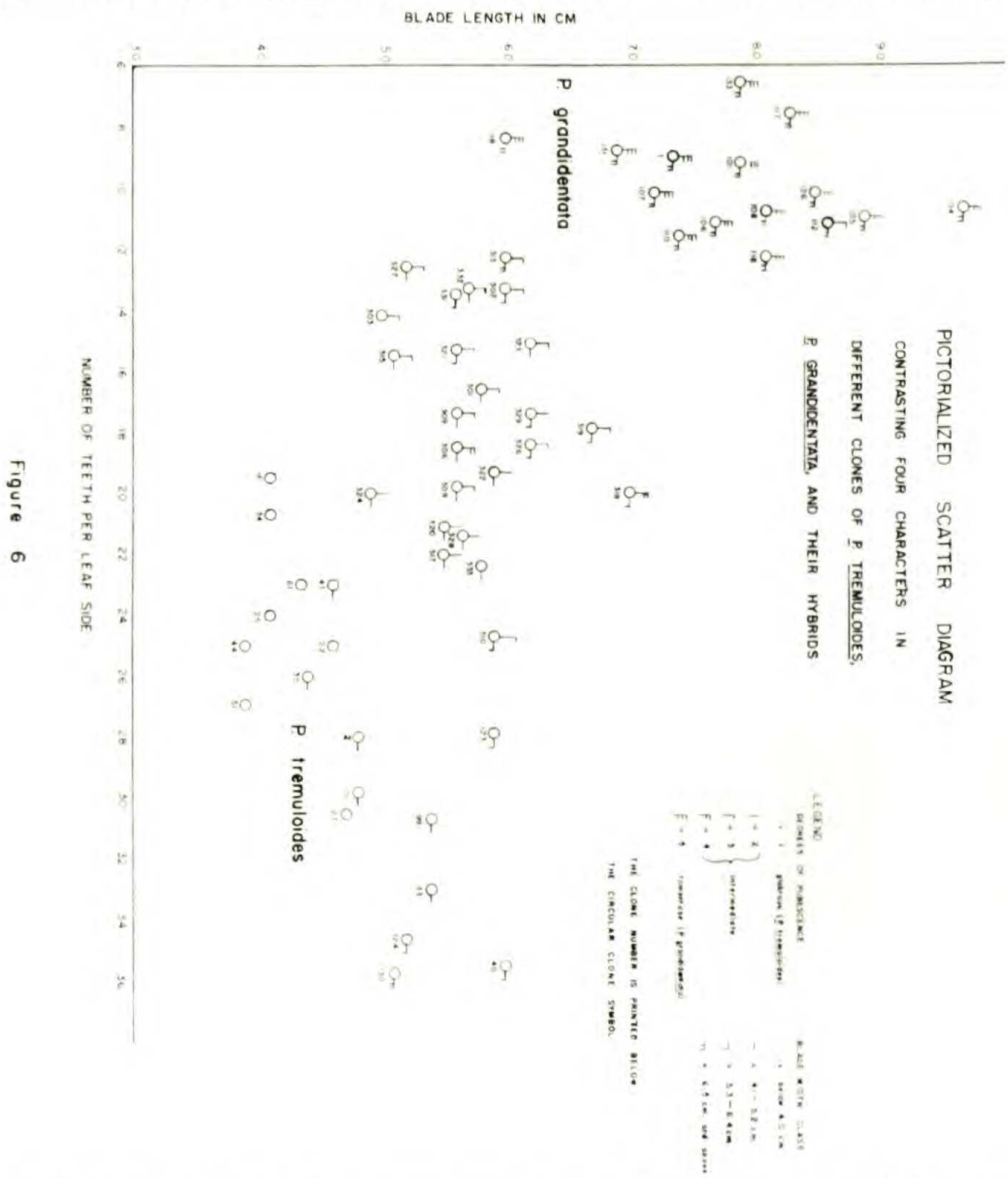


FIG. 6. Pictorialized scatter diagram, contrasting four characters in different clones of *P. tremuloides*, *P. grandidentata*, and their hybrids.

ered on several catkins. Peto (1938) reported that one of the three hybrids near Ottawa, Canada, was "monoecious." An interesting phenomenon observed on one of the catkins from the predominately male hybrid was a row of female flowers proceeding from the base to the tip along one side of the catkin.

The bracts of the aments in the hybrid are characterized by digits that are not as deeply cleft as in *P. tremuloides*, but not as shallow as in *P. alba*. The stigma color of the hybrid (pink) is intermediate between that of its parents. The receptive stigma of *P. tremuloides* is typically red or scarlet, whereas that of *P. alba* is "yellow-green to rose" (Amann, 1956).

POPULUS ALBA × GRANDIDENTATA

One clone of the *alba* × *grandidentata* hybrid was discovered in Section 17, T. 10 N., R. 6 E., Saginaw County. This clone consisted of about 10 to 15 ramets, the largest of which was about 8 inches in diameter at breast height. Victorin (1935) was probably the first to recognize that *P. alba* was hybridizing with the native aspens of Quebec. Heimburger (1936) stated that the *P. alba* × *grandidentata* hybrid was probably the one that Victorin had observed, since the parents flower approximately at the same time. Heimburger (1936) discovered several hybrid trees, and Peto (1938) listed what were apparently seven different clones of this hybrid from Ontario and Quebec. McComb and Hansen (1954) reported two hybrid clones from southeastern Iowa, which were described by Little, Brinkman, and McComb (1957). Subsequently Gatherum (1960) has reported two additional clones from Iowa.

SUMMARY

Thirty-eight clones of the *P. grandidentata* × *tremuloides* hybrid are reported from 10 counties in the Lower Peninsula of Michigan. Although the majority of hybrids have leaf and bud characteristics intermediate between the two parents, three clones are suspected of being introgressants. The reasons for the abundance of hybrids and the greater frequency of hybrid clones in southeastern Michigan than in the northern part of the Lower Peninsula are discussed.

Two clones of the *P. alba* × *tremuloides* hybrid and one clone of the *P. alba* × *grandidentata* hybrid are reported and described.

APPENDIX

Location of *P. grandidentata* × *tremuloides* clones in the Lower Peninsula of Michigan

Clone number	Number of trees in clone	Location
301	5	Section 17, T. 10 N., R. 6 E., Saginaw County
302	13	NW1/4, SE1/4, Section 25, T. 37 N., R. 4 W., Emmet County
303	3	SE1/4, SW1/4, Section 25, T. 37 N., R. 4 W., Emmet County
304	2	Section 6, T. 7 S., R. 7 E., Monroe County
305	2	Section 6, T. 7 S., R. 7 E., Monroe County
306	1	Section 6, T. 7 S., R. 7 E., Monroe County
307	2	Section 6, T. 7 S., R. 7 E., Monroe County
308	4	Section 6, T. 7 S., R. 7 E., Monroe County
309	3	Section 6, T. 7 S., R. 7 E., Monroe County
310	1	Section 6, T. 7 S., R. 7 E., Monroe County
311	1	Section 6, T. 7 S., R. 7 E., Monroe County
312	3	Section 6, T. 7 S., R. 7 E., Monroe County
313	8	NE1/4, Section 33, T. 10 N., R. 5 E., Saginaw County
314	6	S1/2, SE1/4, Section 23, T. 4 S., R. 7 E., Washtenaw County
315	6	S1/2, SE1/4, Section 23, T. 4 S., R. 7 E., Washtenaw County
316	ca. 50	N1/2, NW1/4, Section 28, T. 4 S., R. 8 E., Wayne County
317	ca. 20	N1/2, NW1/4, Section 28, T. 4 S., R. 8 E., Wayne County
318	3	N1/2, NE1/4, Section 30, T. 4 S., R. 8 E., Wayne County
319	1	N1/2, NE1/4, Section 30, T. 4 S., R. 8 E., Wayne County
320	ca. 30	Section 5, T. 8 N., R. 7 E., Genesee County
321	ca. 12	Section 5, T. 8 N., R. 7 E., Genesee County
322	2	SE1/4, Section 17, T. 9 N., R. 7 E., Genesee County
323	3	SE1/4, Section 17, T. 9 N., R. 7 E., Genesee County
324	1	SE1/4, NW1/4, Section 19, T. 7 S., R. 6 E., Monroe County

Clone number	Number of trees in clone	Location
325	1	SE1/4, NW1/4, Section 19, T. 7 S., R. 6 E., Monroe County
326	1	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
327	1	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
328	1	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
329	ca. 50	E1/2, SW1/4, Section 24, T. 7 S., R. 5 E., Lenawee County
330	1	NW1/4, Section 30, T. 6 S., R. 7 E., Monroe County
331	2	SE1/4, NE1/4, Section 33, T. 3 S., R. 9 E., Wayne County
332	6	SE1/4, NE1/4, Section 33, T. 3 S., R. 9 E., Wayne County
333	1	SE1/4, NE1/4, Section 33, T. 3 S., R. 9 E., Wayne County
334	Not recorded	Cedar Lake, Waterloo Recreation Area, near camp, Washtenaw County. (Wagner s.n.)
335	Not recorded	East side Jefferson Rd., Section 15, T. 16 N., R. 2 E., Midland County. (Wagner 8993)
336	Not recorded	Edge of Muskegon State Park, SW1/4, Section 16, T. 10 N., R. 17 W., Muskegon County. (Wagner 9250)
337	Not recorded	North side Water-Munith Rd., Section 15, T. 1 S., R. 2 E., Jackson County. (Wagner 9259)
338	Not recorded	M-83, 4.7 mi. south of Frankenmuth, T. 10 N., R. 6 E., Section 22, Saginaw County. (Wagner 9285)

Literature Cited

Amann, Gottfried. 1956. Bäume and Sträucher des Waldes. Verlag J. Neumann-Neudamm, Melsungen. 231 p.

Anderson, Edgar. 1948. Hybridization of the habitat. Evolution **2**: 1-9.

————. 1949. Introgressive hybridization. John Wiley & Sons, Inc., New York. 109 p.

————. 1953. Introgressive hybridization. Biological Review **28**: 280-307.

————. 1957. A semigraphical method for the analysis of complex problems. National Acad. Sci. Proc. **43**: 923-927.

COOPERRIDER, MIQUAKO. 1957. Introgressive hybridization between *Quercus marilandica* and *Q. velutina* in Iowa. Am. Jour. Bot. **44**: 804-810.

CRITCHFIELD, WILLIAM B. 1960. Leaf dimorphism in *Populus trichocarpa*. Am. Jour. Bot. **47**: 699-711.

DESMARAIS, YVES. 1952. Dynamics of leaf variation in the sugar maples. Brittonia **7**: 347-388.

EINSPAHR, DEAN W., AND PHILIP N. JORANSON. 1960. Late flowering in aspen and its relation to naturally occurring hybrids. Forest Sci. **6**: 221-224.

GATHERUM, GORDON E. 1960. Current tree improvement research in Iowa. Proceedings, 1st Central States Forest Tree Improvement Conf., pp. 16-19.

HEIMBURGER, CARL C. 1936. Report on poplar hybridization. Forestry Chronicle **12**: 285-290.

LITTLE, ELBERT L., JR., KENNETH A. BRINKMAN, AND A. L. MCCOMB. 1957. Two natural Iowa hybrid poplars. Forest Sci. **3**: 253-262.

MCCOMB, A. L., AND NORMAN J. HANSEN. 1954. A naturally occurring aspen-poplar hybrid. J. Forestry **52**: 528-529.

PAULEY, SCOTT S. 1956. Natural hybridization of the aspens. Univ. Minnesota Forestry Note 47, 2 p.

PETO, F. H. 1938. Cytology of poplar species and natural hybrids. Canad. Jour. Res. **16**: 445-455.

STEBBINS, G. LEDYARD, JR. 1950. Variation and evolution in plants. Columbia Univ. Press, New York. 643 p.

VICTORIN, FRÈRE MARIE. 1930. Les variations laurentiennes du *Populus tremuloides* et du P. *grandidentata*. Contrib. Lab. Bot. Univ. Montreal 16. 16 p.

———————. 1935. Flore Laurentienne. Imprimerie de La Salle, Montreal. 917 p.

A DISJUNCT COMMUNITY OF CHESTNUT OAK IN MISSISSIPPI

EDWARD G. ROBERTS

Coker and Totten (1944) and Harrar and Harrar (1946) report the range of chestnut oak (rock oak, rock chestnut oak), *Quercus prinus* L. as being south to Georgia and Alabama. The range map of Munns (1938) shows it in the northeastern tip of Mississippi — Tishomingo County. Mattoon and Beal (1936) report "It is found in the extreme northeastern counties, where it is common on the sandstone bluffs." Lowe (1913) writes of the vegetation of the North-Central Plateau of Mississippi that the typical upland for-